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THE BIOLOGY OF THE CHRYSOMELID BEETLE, *PHYTODECTA OLIVACEA* (FORSTER) (COLEOPTERA: CHRYSOMELIDAE)

By N. Waloff and O. W. Richards
(*Imperial College, London*)

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With 7 Text-figures

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I. Introduction

Phytodecta olivacea (Forster) is common on the bushes of broom, *Sarothamnus scoparius* L., in the grounds of the Imperial College Field Station, Silwood Park, Berkshire. Since 1954 we have been interested in the natural population of this beetle in a colony of broom extending over an area of two acres. A quantitative study is now in progress and an account of it, including the methods used in estimating the fluctuations in the numbers of different stages and the causes determining these fluctuations, will appear in the future. Three sets of samples a week are examined for the eggs and the larvae, the adult population on broom is estimated once a week and that in the soil twice a year—in summer and in the late autumn. At the beginning of this study we found that very little was known about this species and the following is a short account of its biology.

The distribution of *P. olivacea* (Forster) is largely European, although Bedel (1889–1901) says that it also occurs rarely in Algeria. In Great Britain it occurs in England, Scotland and Wales (Fowler, 1890) and in Ireland (Johnson and Halbert, 1902). In the rest of Europe it occurs in Sweden and Finland (Seidlitz, 1891); Denmark (Hansen, 1927); Netherlands (Everts, 1903); Germany (Reitter, 1912); Poland, Silesia (Lomnicki, 1913); all over France (Sainte-Claire Deville and Méquignon, 1935–38); Spain, from the N. coast to Sierra Nevada, Gibraltar (British Museum (Nat. Hist.) Collection); Portugal (de Oliveira, 1867); Switzerland (Stierlin, 1898); Austria (Redtenbacher, 1858); Italy (Porta, 1934); Sicily (British Museum (Nat. Hist.) Collection); Czechoslovakia (Roubal, 1937–41); Hungary (Kuthy, 1918); Greece (British Museum (Nat. Hist.) Collection). There is no mention of *P. olivacea* Forst. in G. G. Yakobson's *Key to Russian Beetles* (1931) and we presume that it is absent from most of the U.S.S.R. We are grateful to Professor A. A. Stackelberg for supplying the information that the specimens in the Zoological Institute, Leningrad are from: Poland—Bodzentin, Novo-Alexandria; Transcaucasia, Geok—Tapa (1 specimen); W. Europe, Germany, France and Spain; N. Africa, Algeria.

We should like to take this opportunity to thank Mr. J. W. A. F. Balfour-Browne for permission to look at the British Museum (Nat. Hist.) collection.

The distribution of *Sarothamnus scoparius* L., the beetle's commonest food plant, is throughout the British Isles except Orkney and Shetland, from Spain to Southern Scandivania, Madeira and Teneriffe (Clapham, Tutin and Warburg, 1952). Bentham and Hooker (1924) give the distribution as chiefly in Western Europe, but extending sparingly to its eastern limits and northward into Southern Sweden.

P. olivacea does not appear to be strictly monophagous and has been reported on *Genista tinctoria* by several authors. Hansen (1927) quotes *Genista tinctoria* as the host plant in Denmark. Kaltenbach (1874) gives the following as the host plants in Germany—*Spartium scoparium, Genista tinctoria, Cytisus laburnum* and *Prunus*. Roubal (1937–41) gives *Sarothamnus scoparius* and *Genista tinctoria* as the host plants in Czechoslovakia, and Schaufuss (1916) says that the beetle occurs on *S. scoparius* and *Genista tinctoria* and is also found on *Prunus padus* in Southern Europe. Bedel (1889–1901) states that in Algeria, where there is no *Sarothamnus*, *P. olivacea* must live on other leguminous shrubs.

At Silwood Park, we have been unable to rear *P. olivacea* on *Ulex europaeus* L. and *Trifolium repens* L., the two commonest plants in the area occupied by *Sarothamnus scoparius*. Our attempts to rear larvae on laburnum leaves were equally unsuccessful.

II. Life History

The life history of the beetle is a long and a fairly complicated one. The adults begin to emerge from hibernation in the soil, in the débris and the grass roots under the broom bushes in April. This emergence continues into May and tails off in June. The adults feed on the broom leaves and oviposit mostly on the upper surfaces of the leaves. The four larval stages also feed on the leaves. The emergence of the adults from the soil is protracted and consequently the oviposition period of the whole population is spread over a period of three

months, from the middle of May to the middle of August. As the result, all the stages occur simultaneously. The fully fed fourth instar larvae descend into the soil, where they pupate and give rise to the second generation of adults, which emerge from August to October. After the middle of June, until the end of August, the adults of the first generation gradually descend back into the soil, where they die, or hibernate for the second season. The beetles of the first, *i.e.* the spring generation, remain on the broom for three to four weeks

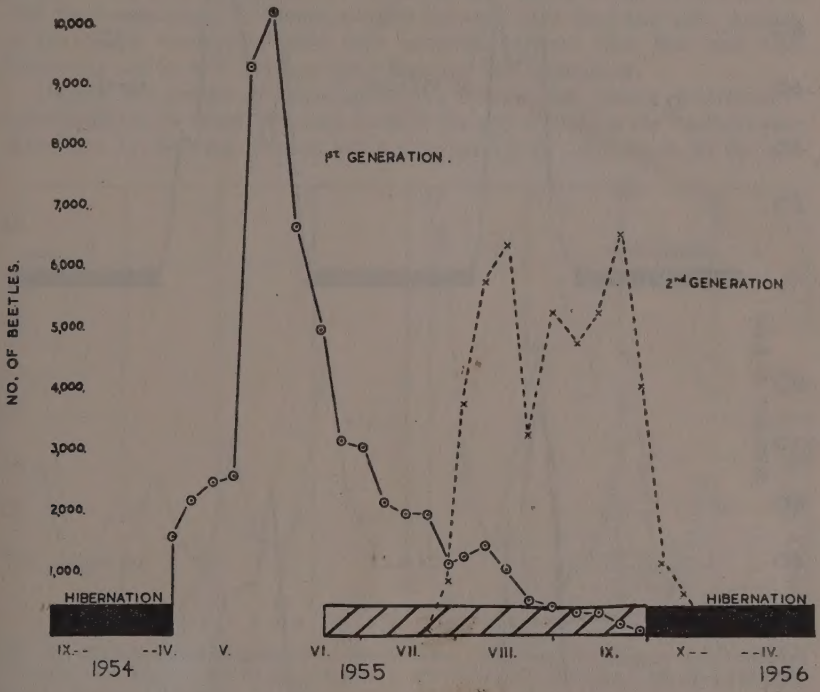

FIG. 1.—Seasonal fluctuations in the numbers of *P. olivacea* adults in a two-acre colony of broom, *Sarothamnus scoparius*. The stencilled block denotes the time of entrance of the survivors of the first generation into the soil; the black blocks indicate the length of time when the adults of both the first and second generations are in the soil.

on the average, though up to 18 weeks in some cases, whereas those of the second generation stay on the bushes for only one to two weeks. They feed, develop large fat bodies but remain sexually immature and enter the soil for hibernation. There is thus a certain overlap of the ovipositing first generation and the non-laying second generation (*see* fig. 1). There is also much simultaneous movement of the population up and down the broom bushes. The fully fed larvae descend into the soil for pupation, the adults of the first generation gradually move back into the soil to die or to enter the imaginal diapause for the second time, while the adults of the second generation ascend the bushes, feed for a

short time and then descend back into the soil for hibernation. Most of the beetles hibernate in the upper 4 cm. of the soil.

Thus the same adults may appear in three successive years, emerging in the autumn of year 1 ; hibernating and emerging in the spring of year 2 ; ovipositing and re-entering hibernation in year 2 ; emerging in the spring of year 3, ovi-

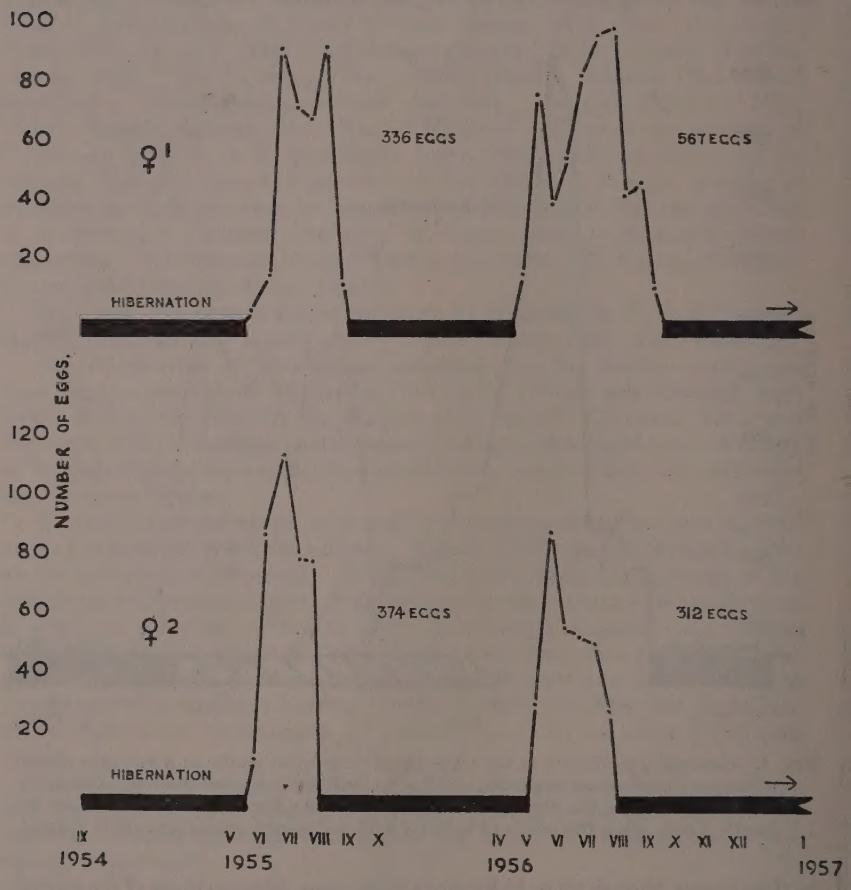

Fig. 2.—The life cycles of two females which oviposited in two successive years. The black blocks indicate the times of imaginal diapause.

positing for the second season and dying in the summer. It is possible that a few beetles may live for yet another season, although so far we have no records of this. The life histories of two females are illustrated in figure 2 where both of them entered hibernation for the third time.

III. Description and Development of Early Stages

The eggs are dirty whitish-yellow, with a lightly sculptured chorion. They are elongated and the average length and width of 20 eggs were 1·3 mm. and 0·5 mm. respectively. Generally they are laid on the leaves, although occasionally the beetles will also oviposit in the grooves of the five-sided broom stems. At the time when the broom pods are still green, the eggs are also laid on them, usually along the hairy margins. The eggs are found on broom almost throughout the duration of the first generation of the beetles and in 1955 they were found in broom samples between 12th May and 12th August. In the colder summer of 1956 they occurred between 28th May and 12th September and in 1957 between 15th May and 2nd September.

During the period of oviposition, the females lay almost continuously throughout the 24 hours, although most of the eggs are laid in the warmest part of the day, *i.e.* between 12 noon and 6 p.m. (*see* fig. 3). A formula for the rate

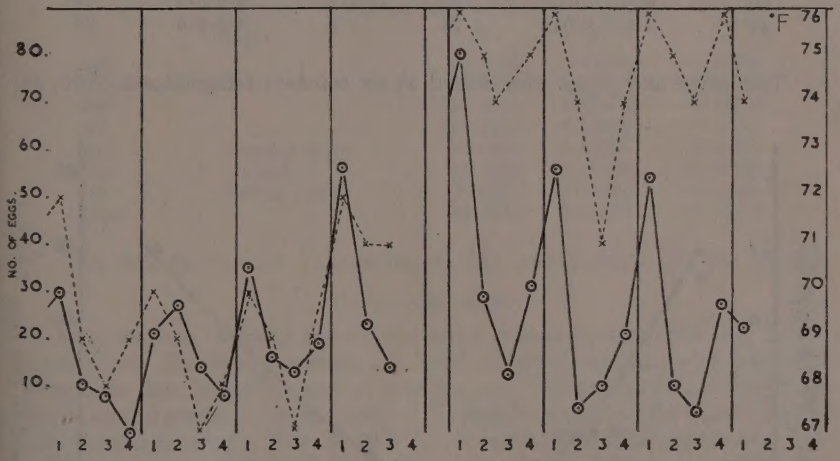

Fig. 3.—Periodicity of oviposition of ten females. The numbers of eggs were recorded every six hours: (1) 12 noon–6 p.m.; (2) 6 p.m.–12 midnight; (3) 12 midnight–6 a.m.; and (4) 6 a.m.–12 noon.

○———○ indicate the number of eggs laid by ten females.

×– – – –× °F.

The first half of the graph was recorded on 8th–13th July, 1955; the second on 14th–18th July, 1955.

of development of the eggs at different temperatures in °C. is given in Table II.

There are four larval instars which feed on the broom leaves. The younger larvae tend to occur most frequently on the tips of the young broom shoots, whereas the older instars are more evenly dispersed amongst the new and the older foliage. The fourth instar larvae, after a period of feeding descend and burrow into the soil, where they pupate after a few days. The freshly hatched first instar larvae are transparent—green with three pairs of anterior black spiracles. Later, the first instar and the subsequent stages have a shiny black head capsule, hairy olive-greyish-green body, blackish-olive green legs,

black spiracles and white hairs. A detailed description of the larvae and of the pupa of *Phytodecta fornicata* Brügg. is given in a paper by Knechtel and Hrisafi (1939), while the larvae of *P. olivacea* have been described by H. van Emden (*in preparation*). The pupae of *P. olivacea* are usually bright yellow, but more rarely they may be green.

Some measurements of the head capsules in the successive larval instars and the total lengths of the larvae were made and are summarised in Table I.

TABLE I.—*Widths of head capsules and total lengths of larvae in mm.*

Instar	Width head capsule (mm.)	Number measured	Body length (mm.)	Limits	Number measured
I	0·48±0·003	76	1·6	1·0–2·1	30
II	0·65±0·004	34	3·2	2·7–3·8	20
III	0·88±0·005	33	4·3	3·2–5·3	12
IV	1·15±0·014	24	7·2	5·1–8·5	20

The larvae and pupae were reared at six constant temperatures of 15, 18,

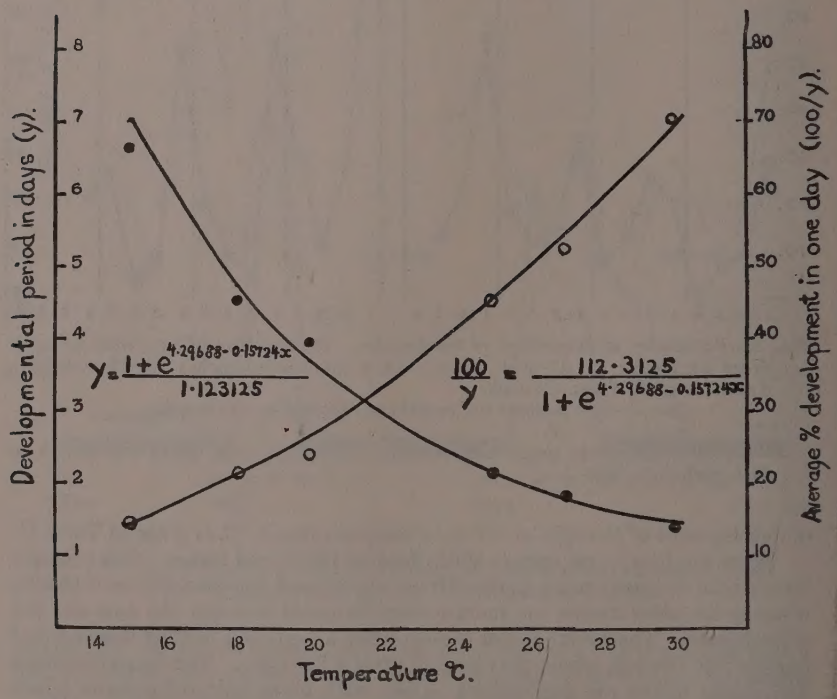
Developmental period in days (y).
Average % development in one day (100/y).
Temperature °C.
$y = \frac{1+e^{4.29688-0.15724x}}{1.123125}$
$\frac{100}{y} = \frac{112.3125}{1+e^{4.29688-0.15724x}}$

FIG. 4.—Observed points on temperature-time curve (closed circles) and temperature velocity curve (open circles) for third instar larvae of *P. olivacea*.

20, 25, 27 and 30 °C. From these data the duration of the stages, y, was obtained and per cent. development per day, *i.e.* $\frac{100}{y}$, was calculated and fitted to the curve having the formula of

$$\frac{100}{y} = \frac{K}{1 + e^{a-bx}}$$

(*see* Davidson, 1944). The data on incubation of the eggs were similarly treated and are also included in Table II. Figure 4 is given as an illustration to these calculations.

TABLE II.—*Davidson's* (1944) *formula fitted to the development of eggs, larvae and pupae*

The duration of development in days (y) *is equal to* $100\ (1 + e^{a-bx})/K$.
x *is temperature in* °C.

Stage	K	a	b
Egg	17·9434	6·87758	−0·45962
1st instar larva	60·7981	4·00859	−0·17986
2nd ,, ,, ...	157·4691	3·67973	−0·11234
3rd ,, ,, ...	112·3125	4·29688	−0·15724
4th ,, ,, (feeding stage) .	76·2355	4·00295	−0·18554
4th ,, ,, (in soil) . .	37·3228	7·50486	−0·40525
4th ,, ,, (whole stage) .	38·0575	3·44422	−0·13486
Pupa	38·3845	3·56649	−0·16588

IV. THE SEX RATIO AND VARIATIONS IN SIZE AND COLOUR OF THE ADULTS

(1) *The Sex Ratio*

As is common to many insects, the males emerge from the soil long before the females. By June the sexes are found in approximately equal numbers. The males then begin to descend into the soil, where they die, or hibernate for the second season. The majority of the females remain on the broom bushes until the late summer. Thus in 1957 the sex ratio of the spring generation was 1 ♂ : 0·06 ♀ in April, 1 ♂ : 0·5 ♀ in May, 1 ♂ : 1·32 ♀ in June, 1 ♂ : 2·73 ♀ in July and 1 ♂ : 4 ♀ in August. However, the totals of males and females which emerge throughout the whole season are approximately equal. Thus in 1954 the ratio in the first generation was 1 ♂ : 0·9 ♀, in second 1 ♂ : 1·7 ♀; in 1955 in the first generation 1 ♂ : 1·3 ♀, in the second 1 ♂ : 1·1 ♀; in 1956 in the first generation, 1 ♂ : 1 ♀, in the second 1 ♂ : 1·2 ♀; in 1957 in the first generation 1 ♂ : 1·4 ♀, in the second 1 ♂ : 1·3 ♀.

In the immature autumn generation the sexes are found in almost equal numbers throughout the whole period of emergence, in other words the male and female larvae and pupae develop at the same rate.

(2) *Variations in the Size of the Adults*

The size of the beetles is extremely variable in both sexes and, while the mean length of 100 females was 4·3 mm., it varied between 3·9 and 5·0 mm. The lengths of 100 males varied between 2·6 and 4·1 mm., the mean being 3·6 mm.

As a rule the females can be distinguished from the males by their greater

size, but in cases of doubt the sexes can be separated by the shape of their maxillary palpus (*see* fig. 5), in which the last segment is broad and securiform in the male (Fowler, 1890).

The means of the weights of field males and females are given in Table III. The weights of the spring beetles are invariably greater than those of the autumn ones, which remain immature until the next season. The differences in the means of the weights of the autumn generation beetles probably reflect the conditions under which the larvae develop, while those of the spring generations may be affected by survival throughout the winter.

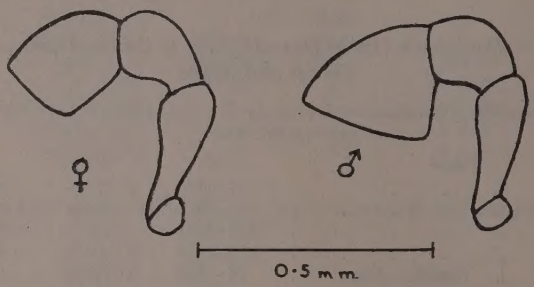

FIG. 5.—The left maxillary palpus of a female and a male beetle. The last segment is broad and securiform in the male.

TABLE III.—*Average weights in mg. of the adults of the field populations*

The numbers weighed are given in brackets.

Generation	Average weight in mg. ♀	♂
1st 1954 . .	11·5 (256)	7·3 (212)
2nd ,, . .	11·1 (106)	7·1 (61)
1st 1955 . .	12·4 (220)	8·2 (229)
2nd ,, . .	11·8 (103)	8·0 (63)
1st 1956 . .	11·9 (245)	7·7 (396)
2nd ,, . .	10·8 (131)	7·4 (97)
1st 1957 . .	12·3 (237)	8·3 (263)
2nd ,, . .	11·3 (170)	7·8 (113)

(3) *Colour Variation in the Adults*

The adults of *P. olivacea*, in common with the other species of the genus *Phytodecta* Kirby, exhibit well marked colour varieties. The most detailed analysis of the variability in the adult pattern in *P. linnaeanus* (Schrk.), *P. viminalis* (L.), and *P. rufipes* (Deg.) has been made by Gause (1930). Gradojević (1953) figures eight varieties of *P. fornicata* Brüggm., and Bechyne (1947) gives illustrations of 181 varieties in the genus *Phytodecta* Kirby.

The three main colour varieties of *P. olivacea* have been distinguished by Fowler (1890) and Reitter (1912), although these authors do not point out the apparent differences in the sexes. The varieties are given as: *v. flavicans* F. entirely rufo-testaceous or yellowish-red; *v. litura* F. rufo-testaceous with

two spots on forehead, the suture of the elytra and a longitudinal band on each, and breast and abdomen black ; *v. nigricans* Weise, colour entirely black or with mouth-parts, base of antennae, forehead and legs rufescent.

In the samples examined by us (about 5000 beetles) all the females were : (i) either entirely yellow-brown, greyish-brown, or pure brown, with a black suture of the elytra. Only the newly emerged, young females of the autumn generation lack the black suture. Black pigmentation develops gradually and there is sometimes a small and variable amount of black pigment on the head and the posterior margin of the prothorax. These females are classified by us as " brown " and are denoted by the letter *b*. This is the commonest variety and about 90 per cent. of the females of the Silwood Park population, exhibit this coloration. (ii) More rarely, the brownish females have not only the suture, but also two lateral lines of the elytra black, with a variable amount of black pigmentation on the head and thorax. This variety is referred to by us as " brown and black " and is denoted by the letters $b + n$ Ventrally, in both varieties the abdomen is black (except in the immature females) and the legs are brown of varying intensity

The males differ from the females in two ways. Firstly, the brown coloration may merge into brick-red or even bright red and both the above varieties (i) and (ii) in the males may have either a brown or a brick-red background. They are correspondngly denoted by the letters b, $b + n$, r, $r + n$. No red females have been found by us, so far. Secondly, there is yet another variety in the males, in which the black lateral bands of the elytra become so expanded as almost, or completely, to obscure the background coloration. This corresponds to *v. nigricans* and is denoted by us by the letter n.

In the same way as the females, the newly emerged males of the summer-autumn generation are uniformly coloured, yellowish- or greyish-brown. The development of the black pigment and sometimes of the red background is gradual and proceeds during hibernation. At the time of spring emergence, the black pigmentation is well marked, but in early spring the red coloration may still be imperfectly developed, some of the males being reddish-brown. Rather more than half the males eventually become red. At the time when the spring and the summer generations overlap, it is possible to distinguish between them by the external coloration, by the internal state of the reproductive organs and by the white or pale buff aedeagus, which becomes heavily pigmented in the older males. Ventrally, the abdomen in the immature males is dark brown,

TABLE IV.—*Percentages of colour varieties in the first generation of beetles*

The numbers examined are given in brackets

♀	*b*	*b* + *n*	*r*	*r* + *n*	*n*
1954 (588)	90·5	9·5	.	.	.
1955 (739)	87·1	12·9	.	.	.
1956 (986)	86·4	13·6	.	.	.
1957 (397)	93·9	6·1	.	.	.
♂					
1954 (627)	17·4	22·0	1·4	59·2	0·0
1955 (557)	10·8	28·7	8·7	43·8	8·0
1956 (878)	4·1	28·1	4·1	60·7	3·0
1957 (479)	7·3	19·8	4·8	64·3	3·8

but it blackens rapidly; the head, thorax and the legs are also pale brown in the recently emerged males, but they darken throughout hibernation. The legs are eventually of different shades of dark brown, and occasionally they may be wholly black.

The proportions of the colour varieties found at Silwood Park are summarised in Table IV. It will be noted that, in contrast to the females, the majority of the males (over 80 per cent.) are characterised by the development of the black pigment on the elytra.

V. The Female Reproductive System

The structure of the female reproductive system of *P. olivacea* is similar to that of *P. fornicata* Brügg., described in some detail by Voukassovitch (1939). The ovary is acrotrophic, typically with 10 ovarioles on each side, this number varying between 8 and 12. The variation in 40 ♀ was as follows: 8 + 8 in 2, 8 + 9 in 3, 9 + 9 in 1, 9 + 10 in 3, 10 + 10 in 27, 10 + 11 in 1, 11 + 12 in 1 and 12 + 12 in 2. The reproductive system is characterised by the absence of spermatheca and this, according to Hagan (1951), is one of the characteristics of the ovoviviparous insects. Rethfeldt (1924) has shown in *Chrysolina varians* (Fab.), a species with the same type of reproductive system, that the sperm is stored between the last unripe ovum and the last two eggs which contain embryos. The tendency towards viviparity, which occurs in several genera of Chrysomelidae (Hagan, 1951), has been established in several species of the genus *Phytodecta*. It was shown by Williams (1914) that *P. viminalis* (L.) is viviparous, while in *P. rufipes* (Fab.) the chorion ruptures shortly after oviposition (Henneberg, 1927). In two American species, *P. affinis* (Gyll.) and *P. pallidus* (L.), the larvae hatch five minutes after the eggs are laid (Notman, 1921). In most species ovoviviparity appears to be facultative and it is probable that under certain conditions it may occur in *P. olivacea* as well. In the laboratory, one female laid eggs which hatched in under 24 hours and on one occasion four out of a set of 22 field females, collected and dissected on 16th July, 1954 had eggs in the ovarioles with well advanced larvae, in which the ocelli and the black spiracles were clearly discernible. Although over 800 mature females have been dissected up to date, this condition has never been seen again. Similar facultative ovoviviparity in *P. fornicata* has been described by Voukassovich (1939). It is assumed that in *P. olivacea* this tendency is only rarely realised, as the hatching period of the eggs in out-door conditions is long and varies with the temperature, generally between six and ten days (*see* Table II).

VI. Seasonal Changes in the Reproductive System, and Imaginal Diapause in *P. olivacea*

In the second, *i.e.* in the summer-autumn generation of the beetles, the ovaries remain undeveloped and the females enter the soil for hibernation with an undifferentiated germarium and an enormous flocculent fat body. In the following spring, the females mature within 8 to 10 days after emergence. In the mature females, egg 1 is much bigger than egg 2, and only three or four ovarial rudiments are differentiated at a time in an ovariole. Females which have oviposited have clearly discernible corpora lutea at the bases of the ovarioles. Singh (1954) examined the structure of the corpora lutea of *P. olivacea*

histologically and found that they consist of highly pycnotic follicle cells undergoing autolysis, with crumpled tunica propria forming a ring on top. We have seen in weekly dissections of mature females that the means of the number of ripe eggs vary between 8·8 and 13·8, although in a few females this number was as high as 20–23. In other words, only rarely do all the ovarioles function simultaneously. The fat body in the laying females is much smaller than in

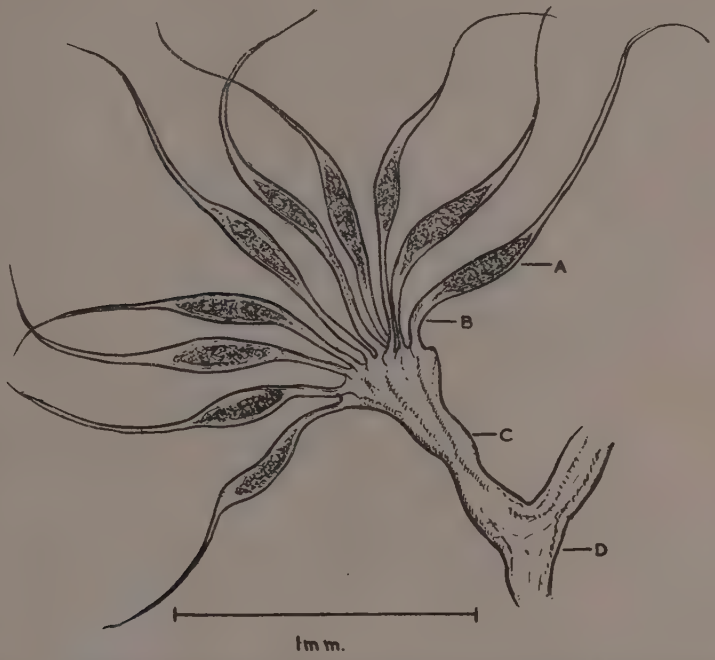

Fig. 6.—The reproductive system of an immature female, diapausing for the first time. (*A*) undifferentiated germarium, (*B*) pedicel, (*C*) R. oviduct, (*D*) vagina.

the immature ones, as well as in the mature beetles preparing to hibernate for the second time. In the females which survive and enter imaginal diapause for the second season, the ovaries gradually regress until the oocytes are resorbed, leaving only the germarium and traces of corpora lutea at the bases of the ovarioles. The reproductive organs of the females with regressed ovaries remain larger than those in the immature beetles, hibernating for the first time. In *Dytiscus* (Joly, 1945) and *Leptinotarsa* (De Wilde, 1953) the oocytes pass through cycles of growth and degeneration during the imaginal diapause. It is not yet known whether similar cycles occur in *P. olivacea*, and so far no traces of oocytes have been found in the ovaries of the diapausing beetles. In *Dytiscus* the complete growth of the oocytes has been shown to be under the control of the hormone from the corpora allata, this activity of the glands in turn being dependent on a stimulus from the brain mediated by the corpus cardiacum.

The males of *P. olivacea* also tend to have larger fat bodies prior to hibernation. During the period in which the two generations of the beetles occur simultaneously in the field, the young emerging males can be distinguished from the old ones, not only by the difference in the external coloration, but also by their small white testes, which are yellow or orange in the mature males and by the white, or only lightly pigmented aedeagus, which is brownish-black, or black in the old beetles.

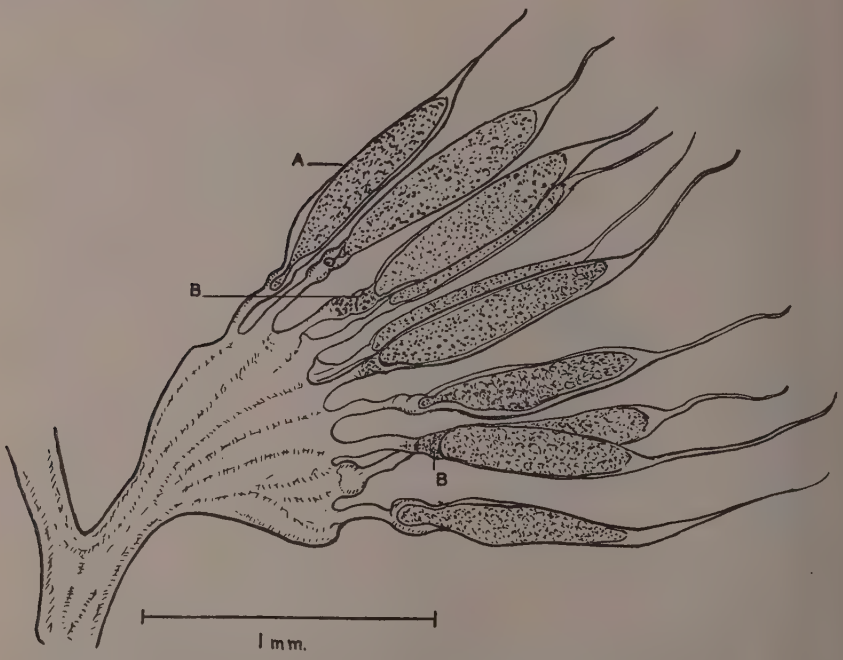

Fig. 7.—The reproductive system of a female with regressed ovaries, diapausing for the second time.

Table V.—*Condition of the ovary and the fat body in* (*a*)—*the females of the spring generation, and* (*b*)—*females of the autumn generation*, 1954

	(*a*)					(*b*)		
Date	Number dissected	Number mature	Average number ripe eggs in ovaries	Average value fat body	Date	Number dissected	Number mature	Average value fat body
31.v	26	25	13·8	1·3	30.viii	14	0	2·3
8–15.vi	108	105	11·4	1·1	8–13.ix	50	0	2·0
21–28.vi	61	58	12·5	1·2	20–27.ix	40	0	2·8
16–26.vii	40	36	10·0	1·5	4–11.x	27	0	2·8
					18–25.x	14	0	3·2

The condition of the ovaries and the fat body throughout the active period is summarised in Table V. The arbitrary values assigned to the fat body were : 4, denoting a fat body filling all the available space of the haemocoele ; 3, large ; 2, small ; 1, traces of fat. When fat was altogether absent, its value was denoted by 0. It is yet too early to say whether the imaginal diapause is in direct response to the changes in the external factors. Diapause in this species is not brought about by a fall in temperature, as most of the insects of the first generation enter the soil throughout June and July and both the first and the second generation beetles kept in a constant temperature room at 25° C. entered hibernation more rapidly than did the ones kept at room temperature. The possibility that the rise in temperature may induce diapause may also be excluded, as the second generation of beetles enters diapause throughout August, September and throughout the first half of October. As is common to many insects in Great Britain, towards January, *i.e.* after the beetles have experienced low temperatures in out-door conditions, it is possible to bring them out of diapause by exposing them to high temperature, and in a constant temperature of 25 °C., the beetles will at this date emerge, pair, mature and oviposit. The possible effects of the day length on the imaginal diapause (*see* Lees, 1955) are being investigated and, although these experiments are in preliminary stages, it is interesting to note that a small number of the second generation females have responded to an increased illumination of 16 hours in the autumn and winter months, while so far, the males have failed to do so. The females may mature and oviposit but lay sterile eggs, unless they are fertilised by the surviving males of the first generation.

VII. Oviposition

(1) *Copulation, Pre-oviposition Period and the Length of the Oviposition Period*

After emergence in the spring, the beetles copulate almost at once. Copulations in *P. olivacea* are frequent and one pair in the laboratory was recorded *in copula* on seven separate occasions. Pairing lasts about half an hour. In the autumn, when the two generations of beetles overlap, the few old males remaining above the soil copulate equally freely with the old females and with the immature ones of the second generation. However, these females remain immature and enter hibernation. The new generation males do not copulate until the following spring.

The length of the pre-oviposition period varies with temperature and in 43 laboratory females its average was 8·2 and its limits 4–20 days. During this period the females feed avidly and their weight increases by about 35 per cent. of that on emergence. Thus the average weight of 30 females emerged after hibernation was 9·0 mg. (with the limits of 6·0–11·5 mg.), while their average on the first day of oviposition was 12·2 (limits 10·0–15·0 mg.). The length of oviposition period of 74 laboratory females was 65·5 days. In 16 females kept under observation in 1954 it was 68 days, in 32 females in 1955 it averaged 67 days and in 26 females in 1956 it was 65·5 days.

The average number of eggs laid by 26 females in 1956 was 320, nine of them laying over 400 (417–678). In 1955, the 32 females laid an average of 269, five of them over 400 (415–603), while the average in 1954 was lower, and

the 16 females under observation laid an average of 251 eggs, the maximum being 399.

Laying is almost continuous throughout the period of oviposition and the commonest number of eggs laid in 24 hours lies between two and six, while the greatest number laid was 21 (*see* Table VI).

TABLE VI.—*The frequency of the numbers of eggs laid in* 24 *hours by* 50 *laboratory females*, 1955

Number eggs in 24 hr.	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	21
Number of records	180	48	146	150	158	145	141	119	69	50	53	33	28	20	7	5	3	2	1	1	1

Some of the females survive the second winter and oviposit for the second time. The total fecundity of ten such females is given in Table VII. It

TABLE VII.—*Fecundity of* 10 ♀ *of* P. olivacea, *ovipositing in two successive seasons*

Total fecundity in 1st season .	336	603	282	374	153	364	226	139	76	64
„ „ „ 2nd „ .	567	158	428	312	498	229	185	113	153	138

will be seen that three of the females laid more eggs in the first season, three in the second, and the remaining four laid approximately equal numbers in the two successive years. Thus the average fecundity of ten females in the first year was 262 and that in the second year 288. The greatest total fecundity of a female ovipositing in two successive seasons was 903 (*see* fig. 2).

(2) *Total Fecundity of* P. olivacea

(i) The number of eggs laid is directly related to the length of the oviposition period and this is clearly seen in Table VIII. Thus it would seem that the

TABLE VIII.—*Relation between the length of oviposition period and the number of eggs laid*

Oviposition period (days) .	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139
Average number eggs per female	43	94	166	201	254	261	341	397	414	518	433	500	547
Number of females (95) .	2	3	9	22	16	10	7	4	7	7	2	4	2

factors which delay the onset of imaginal diapause in *P. olivacea*, also directly or indirectly affect the total number of eggs laid.

(ii) The weight of mature females also affects the fecundity of the beetles. The effect of mature weight on the total number of eggs laid was analysed in 38 females; the relation between these two factors was significant ($P < 0{\cdot}05 > 0{\cdot}02$). The calculated slope of the regression line, or b, was equal to 30·1358; in other words an increase of 1 mg. in mature weight denotes an increase of about 30 eggs in the completed oviposition.

(3) *Daily Oviposition Rate*

The effect of temperature on oviposition is marked, but both in the laboratory and in the field it is complicated by the effects of the age of the females. The older females lay fewer eggs within each season, although the total fecundity of those females which survive and oviposit in two successive summers does not differ appreciably from one year to the next. Table IX illustrates the fall off in the rate of oviposition by the older females, as it shows that, in spite of the rise in temperature in the second half of the oviposition period of 12 laboratory females, the number of eggs rose to a peak and then fell off with time.

TABLE IX.—*Weekly oviposition by* 12 *laboratory females* (1955)

Week	Average number eggs per ♀	Average temp. (°F.)	Week	Average number eggs per ♀	Average temp. (°F.)
1	5·7	60·0	9	35·3	66·6
2	24·5	61·4	10	33·2	64·0
3	26·3	59·3	11	28·8	72·3
4	26·0	60·6	12	23·9	71·4
5	25·3	62·3	13	30·4	69·4
6	33·5	63·9	14	31·0	70·0
7	31·1	62·9	15	21·0	65·7
8	41·3	65·4	16	16·8	68·3
			17	7·3	72·4

From the laboratory data regression equations relating the number of eggs laid in 24 hours (y) with the temperature during this period in °F. ($t°$) and the age of the female in days (d), where $d = 1$ on the first day of oviposition, have been worked out for two successive seasons, 1954 and 1955.

The equations take the following form:

1954

$$y = -0{\cdot}02974\,(d) + 0{\cdot}14568\,(t) - 4{\cdot}62983 \quad . \quad . \quad . \quad (1)$$

1955

$$y = -0{\cdot}02603\,(d) + 0{\cdot}14235\,(t) - 3{\cdot}80829 \quad . \quad . \quad . \quad (2)$$

Significance of the regression coefficients was as follows: in (1) P for $(d) < 0{\cdot}001$ $(n = 96)$; P for $(t) < 0{\cdot}01$ $(n = 96)$ and in (2) P for $(d) < 0{\cdot}001$ $(n = 116)$; P for $(t) > 0{\cdot}01 < 0{\cdot}02$ $(n = 116)$.

Substituting the values for days and for temperature in these equations, one can calculate the probable oviposition of the females. This is illustrated in Table X. Thus a rise of 20° F. doubles the number of eggs laid. The con-

TABLE X.—*Calculated value of the numbers of eggs laid by a single* ♀ *from equations* (1) *and* (2)

	50° F.		60° F.		70° F.	
On day	1954	1955	1954	1955	1954	1955
1	2·6	3·3	4·1	4·7	5·5	6·1
10	2·4	3·0	3·8	4·5	5·3	5·9
20	2·1	2·8	3·5	4·2	5·0	5·6
30	1·8	2·5	3·2	3·9	4·7	5·4

sistently greater number of eggs laid by the 1955 females, observed both in the laboratory and in the field, may be at least partly related to their greater weight. In 1954 the average weight of 256 field females of the first generation was 11·5 mg., whereas in 1955 that of the 220 field females was 12·4 mg. The weights of the males in the two consectutive years varied in the same direction, they were 7·3 mg. (212 males) in 1954 and 8·2 (229 males) in 1955. Variations in fecundity cannot, however, be explained by weight and temperature alone, as in 1956 the average weight of the females of the first generation was 11·9 mg., yet they laid more eggs than in the two previous years.

Some idea of the possible effects of nutrition on fecundity was obtained from the following experiments. From the middle of June the foliage on the broom bushes can be subdivided into " leaves on young shoots " and the broader, darker, " old leaves ". Thirty-three females collected in the field were fed on old leaves for three days (28th June to 1st July, 1955), and the daily oviposition of each female was recorded. The beetles were then subdivided into three groups (11 females in each) which had produced the same total number of eggs in the preceding period. Thus, the females of group A laid 118 eggs, those of group B 118 eggs and those of group C 117 eggs. The beetles of group A were continued on the diet of old leaves for another two periods of three days, those of group B were transferred on to a diet of new leaves on young shoots, and group C on to fresh green pods. The rates of oviposition of the three groups

TABLE XI.—*Oviposition on old leaves, young green shoots, and green pods by* 3 *groups of beetles* (11 ♀ *in each*), 1955

	28.vi–1.vii			2.vii–4.vii			5.vii–8.vii		
Group	Food	Av. °F.	Eggs/ ♀/day	Food	Av. °F.	Eggs/ ♀/day	Food	Av. °F.	Eggs/ ♀/day
A .	Old leaves	64·7	3·6	Old leaves	62·3	4·5	Old leaves	67·3	6·5
B .	„ „	64·7	3·6	New leaves	62·3	5·2	New leaves	67·3	8·2
C .	„ „	64·7	3·6	Green pods	62·3	0·9	Green pods	67·3	0·6

are summarised in Table XI. The low number of eggs on the green pods is of little interest, as the beetles encountered mechanical difficulties in feeding on them and chewed only the thinner edges. A somewhat larger number of eggs laid on the diet of growing leaves may be of interest, although the experiments will have to be extended. Grison (1952) has shown conclusively that in *Leptinotarsa* the ageing of the food plant leads to a fall in egg production.

VIII. SUMMARY

The active stages of the life history of *Phytodecta olivacea* (Forster) are passed on broom, *Sarothamnus scoparius* L., and the inactive stages in the débris and the upper layer of the soil under the bushes. The eggs are laid on the leaves and the four larval instars and the adults feed on the foliage. Pupation is in the soil. A new generation of beetles emerges in late summer and autumn; they feed, but remain immature and enter hibernation in the soil. The adults emerge the following spring, oviposit and enter the soil again in a state of imaginal diapause. The survivors emerge in the following spring and

oviposit for the second season. Thus the same individuals may appear in at least three successive years and the adult populations are of mixed ages.

The adults fall into three colour varieties, there being sexual dimorphism in the background coloration and in the amount of development of black pigment.

The ovarioles are acrotrophic and typically 10 + 10 in number. There is no spermatheca, a state characteristic of ovoviviparous insects. It is considered that *P. olivacea* is facultatively ovoviviparous.

Fecundity is dependent on the weight of the mature females and on the length of time they spend on the broom bushes, while the daily oviposition rate is influenced by temperature and by the age of the females. The average numbers of eggs laid in the laboratory in three successive years were 251, 269 and 320. The greatest number of eggs laid by a female in one season was 678, and that by a female surviving and ovipositing for two successive summers was 903 (336 and 567).

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